CHONDROMYCES THAXTERI, A NEW MYXO-BACTERIUM

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(with plates V and VI)

The Myxobacteriaceae constitute an extremely interesting assemblage of forms, because of their apparent relationship to the bacteria on the one hand, and to the slime molds, particularly the Acrasieae, on the other hand. The individual plants are bacteria-like rods in all cases, and after a vegetative period these swarm together to organize a definitely shaped pseudo-fructification, without, except in the one genus *Myxococcus*, undergoing any marked morphological changes themselves. These fructifications are not comparable to the more or less heaped up colonies characteristic of certain bacteria, but, as Thaxter (9) has pointed out, are strictly comparable to the "fructifications" of the Acrasieae, the only other group in which there exists "a similar concerted action of aggregates of individuals toward a definite end, namely, the production of a more or less highly differentiated resting state." Whether they are to be regarded as a family of bacteria or as a division of the Myxomycetes, close to, if not included within the Acrasieae, remains undecided. Baur (1) and Quehl (4) and more recently Pinoy (3) incline strongly to the former view; Vahle (10) and others incline to the latter view.

Of the fewer than 30 known bona fide species, distributed among 3 genera, 11 have been referred to the complex and variable genus *Chondromyces*. The one described in this paper adds another, *Chondromyces Thaxteri*, n. sp., in some respects the most remarkable of all. This form appeared in small quantity on deer dung from Algonquin Park Forest Reserve, Ontario, and was successfully cultured for more than two years, or until the identity of the species was established, when it was allowed to die out.

The fructifications, or more properly pseudo-fructifications, are ordinarily yellowish, but may vary from flesh-colored to reddish orange, in this as in other respects showing great variability, and ranging 250–750 μ in height, averaging about 350 μ. They are usually simply stalked, but the stalks may fork or even branch more than once, as is shown in fig. 5. The stalks are broad-based, narrowing slightly toward the apex, and yellowish in color. Within their gelatinous matrix are considerable numbers of rods, especially in the lower part. It may be noted also that many members of the colony contributing to the fructification are left on the medium in the immediate neighborhood.

At the tip of the stalk a single head of rods may be found, but more frequently several are formed, resulting from a lobing or branching of the mass that has attained this level, an example of which is represented in fig. 3. These lobes or heads may be sessile or short-stalked. This habit calls to mind *C. pediculatus* Thaxt., in which species the lobes at once ripen as the ultimate cysts, and *C. catenulatus* Thaxt., in which, however, the lobes first elongate and then contract at intervals, due to secondary movements of the rods, giving rise to chains of cysts. But development goes further here. A striking phenomenon next takes place, namely, a heaping up of the rods in radially arranged masses over the entire surface of each head, in the form of elongated cones (figs. 7, 11) or, more rarely, in the form of cylinders (figs. 4, 12), likewise of comparatively great length. In the first instance the apices of the cones are often attenuated to such an extent as to be tipped with but single rods. The surface of the now bristling head is directly invested closely by a yellowish transparent membrane, a secretion from the rods.

The cylindrical form has its counterpart in *C. crocatus* B. and C., in which, however, the cylinders become sharply abstricted at the base, and mature as cysts, when ripe falling away from the cystophore and from one another at the slightest touch; and similarly the conical form, which is the more frequent of the two, recalls *C. apiculatus* Thaxt., possibly its most closely related species. In *C. apiculatus* the cones develop into cysts as do the cylinders in *C. crocatus*, but this is first initiated by a secondary migration of the rods to the centers of the cones, the covering membrane simply shrivelling at the bases and apices.

In *C. Thaxteri* the purpose of the cone and cylinder formations is not evident, for immediately succeeding the completion of the envelope there is a migration of the rods back to the center of the head, within which they form a smooth, more or less spherical mass, the membranes of the protuberances persisting as somewhat shrivelled and twisted or striated appendages, containing no rods except such occasional stragglers as may happen to have adhered to their inner surfaces.

The bristly heads, without further morphological changes, then mature as cysts, which drop off almost as lightly as do the spore-like cysts of *C. crocatus*. Figs. 3, 4 or 7, 9, and 1 represent in sequence the stages that have been described. The course of development just outlined is entirely independent of variations in moisture, food supply, light, and temperature, so far as I have ever observed; always the formation of cones or cylinders on the surfaces of the heads, and their subsequent abandonment, the rods retreating over the route along which they came. The ripening of the head is completed by a movement of rods away from the short stalk, and a shrivelling or contraction of the membrane at that point, which thus explains in part the mode of dehiscence (fig. 1).

The number of cysts, as already indicated, varies from one to several, usually 3–4, but sometimes there may be as many as 20–30. Not infrequently fusions take place in the early stages between neighboring developing heads, as shown in fig. 2. When mature, the cysts are spherical or more commonly depressed spheres or thick disks, and average about 140 μ in extreme width, though varying from 65 to 165 μ. These measurements include the appendages, which vary from 30 to 15 μ in length, and from 10 to 22 μ in breadth at their bases.

On germination of the cysts the rods swarm out through the basal scar of the membrane, leaving the bristly empty husk behind. Fig. 14 indicates the way in which this process takes place, and also shows that the appendages on the membrane have been septated off in no way by an inner secondary membrane.

Attention has already been called to the many variations exhibited by *Chondromyces Thaxteri*, a phenomenon shared to some extent by other species; variations in color, striking variations in every dimension of the fructification, variations in the branching of the stem, and in the number and size of the cysts and their appendages. Compare, for example, figs. 1, 2, 5, 8, 9, and 10. Many species might easily be based on a series of mounts made from a single culture. There is no doubt, of course, that these are simple fluctuating variations of very wide range. It is also almost certain, although not demonstrated, that many of these are due to environment; the local differences of food supply and moisture on the substrata on which they grow cannot be inconsiderable; but this does not explain all.

The life history was followed carefully throughout in its main features, and was found to conform closely to the account given by THAXTER for *C. crocatus*. Confirmation is given also of the fact that the contents of the rods are characterized by deeply staining masses, especially just before and during the resting stage, one to three or four being readily demonstrable. Eosin differentiates them especially well in the cystophores, where the imbedded rods, stained deep pink, stand out in striking contrast to the yellowish translucent matrix. This stain also brings out the uneven distribution of the rods in the cystophore; often there is a thin outer zone almost free from them, and, too, they are much more abundant toward the base than elsewhere, gradually diminishing in number toward the apex. The contents of the cysts stain deeply; the envelope remains unstained, chitinous yellow in appearance, showing for the cysts at all events that the color is not restricted to the rods, as stated by BAUR.

Many attempts were made to secure pure cultures, and a variety of media was employed. The only one that yielded tolerable results was the natural substratum of the organism. Moreover, even on this it was impossible to secure good results if the cysts alone were planted. There was always an admixture in flourishing cultures. What relation the impurities bore to the *Chondromyces* I did not determine. It may be a case of succession of floras, in which the ground must first be prepared for the *Myxobacterium*. So far as I have been able to learn, the same feature is true of other species that have been cultivated. PINOY (3) has recently investigated this feature of *Chondromyces crocatus*, and he announces that a *sine qua non* condition for obtaining a complete development of the fructification is the presence of a special bacterium, a *Micrococcus* related to *M. latens*. He demonstrated this by first isolating the coccus and then planting it alongside rods of *Chondromyces* on the surface of the same sterilized medium. It was only where the resultant colonies grew together and mingled that perfect fructifications of *Chondromyces* were formed, although the relation does not appear to be lichenicolous in character. He affirms that if the *Micrococcus* be present, normal cultures can be obtained on many different kinds of media. I know of no further observations on this subject. ZEDERBAUER (11) cannot be quoted, because he was not working with Myxobacteriaceae as he supposed. In my own cultures a filamentous fungus with septate hyphae was constantly present in small amount, and not infrequently the threads of this fungus are imbedded in the cystophore, although never in the cysts. But ample observations make certain that whatever rôle it plays, if any, it is not a necessary constituent of the fructification at any stage.

The species of *Chondromyces* that have been so far described constitute a rather close evolutionary series; and the outstanding character in which the evolutionary forces are manifested is fundamentally not one of form, size, or color, but of movement. Thus we may begin with a form like *C. muscorum* Thaxt., in which single, simple, unstalked cysts are formed. In *C. serpens* Thaxt. and *C. lichenicolus* Thaxt. there is a movement in a horizontal direction, resulting in sessile, elongated, and often confluent, coil-like cysts. The primary movement is vertical in *C. gracilipes* Thaxt. and a simple stalked cyst results. In some species there may be a forking of the stalk, but in most cases there is a radial movement from the primary stalked mass, resulting in the formation of heads of small cysts, for example, in *C. crocatus*. In these cysts there may be secondary migrations, a single one toward the center of the cyst in *C. apiculatus* Thaxt., or several, the centers of migration being separated at intervals in a radial line. The last is illustrated by *C. catenulatus* Thaxt., with its heads of cysts in chains.

In the ontogeny of *C. Thaxteri* every stage in the vertical and radial line of evolution relative to this phenomenon of movement is traversed, and then there is a beginning of a migration of the rods back over the same road before maturity is reached; and this order of development is invariably followed regardless of the conditions of the environment. As the secondary movement in *C. Thaxteri* carries the rods entirely out of the structures that apparently correspond to the cysts of *C. crocatus*, *C. apiculatus*, etc., it seems reasonable to conclude that *C. Thaxteri* stands at the extreme end of the main evolutionary branch of the genus as we know it at present.

Chondromyces Thaxteri, sp. nov.—Pseudoplasmodiis luteo-vel carneo-coloratis; baculis 3–6 $\mu \times 0.5$ μ longis; fructificationibus luteis, 250–750 μ, vulgo circa 350 μ altis; stipitibus plerumque simplicibus, atque interdum ramosis; cystes setaceas, sub-globosas, breviter pedicellatas vel sessiles, 1–7 vel plures numero gerentibus; quae cystes integrae 65–165 μ, vulgo circa 140 μ latae sunt; setae autem sunt conicae, 15–30 μ longae et ad bases 10–12 μ latae.—In fimo cervino nascens in Algonquin Park, Ontario, Canada.

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EXPLANATION OF PLATES V AND VI

FIGS. 1, 2, 5, 8, 9.—Mature "fructifications" of *Chondromyces Thaxteri;* ×240.

FIG. 3.—An immature stage; ×240.

FIGS. 4, 7.—An immature stage, but later than the one in fig. 3; they represent the cone or finger-like processes formed on the "heads" of the fructification; ×240.

FIG. 6.—An early stage in the heaping up of the rods; ×240.

FIG. 10.—Cysts on the left hand branch are mature, those on the right are rather younger than the ones represented in fig. 3; ×195.

FIGS. 11, 12.—Processes from figs. 7 and 4 respectively, drawn on a larger scale; ×720.

FIG. 13.—Part of a mature cyst (fig. 8) on a larger scale, showing empty husks of processes after rods have migrated back from them; ×720.

FIG. 14.—A germinating cyst; ×720.